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Life history influences how fire affects genetic diversity in two lizard species

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Running title: Fire effects on lizard genetic diversity

Abstract

'Fire mosaics' are often maintained in landscapes to promote successional diversity in vegetation with little understanding of how this will affect ecological processes in animal populations such as

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dispersal, social organisation and re-establishment. To investigate these processes, we conducted a replicated, spatio-temporal landscape genetics study of two Australian woodland lizard species (*Amphibolurus norrisi* (Agamidae) and *Ctenotus atlas* (Scincidae)). Agamids have a more complex social and territory structure than skinks, so fire might have a greater impact on their population structure and thus genetic diversity. Genetic diversity increased with time since fire in *C. atlas* and decreased with time since fire in *A. norrisi*. For *C. atlas*, this might reflect its increasing population size after fire, but we could not detect increased gene flow that would reduce loss of genetic diversity through genetic drift. Using landscape resistance analyses, we found no evidence that post-fire habitat succession or topography affected gene flow in either species and we were unable to distinguish between survival and immigration as modes of post-fire re-establishment. In *A. norrisi*, we detected female-biased dispersal, likely reflecting its territorial social structure and polygynous mating system. The increased genetic diversity in *A. norrisi* in recently burnt habitat might reflect a temporary disruption of its territoriality and increased male dispersal, a hypothesis that was supported with a simulation experiment. Our results suggest that the effects of disturbance on genetic diversity will be stronger for species with territorial social organisation.

Keywords

Biodiversity conservation; dispersal; disturbance; fire regime; landscape genetics; reptile

Introduction

Fire is a natural driver of ecological dynamics, but modern changes in land use have altered fire regimes in ecosystems around the world (Butz 2009; Regan *et al.* 2010). Some animal species are threatened by recent increases in the extent and frequency of fire (Lyet *et al.* 2009; Sanz-Aguilar *et al.* 2011), while others decline with less frequent fires (Templeton *et al.* 2011). Fire management

often combines prescribed burning and fire suppression to maintain 'fire mosaics', assuming that successional diversity in vegetation will benefit biodiversity overall (Parr & Andersen 2006). However, there is little understanding of the spatial and temporal scales at which fire mosaics allow animal species to persist in a landscape (Kelly *et al.* 2012; Nimmo *et al.* 2013).

Fire, or lack of fire, can fragment suitable habitat for some animal species (Neuwald & Templeton 2013) by imposing barriers to dispersal (Levy *et al.* 2010; Prevedello *et al.* 2010). Extinction risk may be elevated in populations fragmented by fire mosaics through declines in genetic diversity and population fitness (Frankham 1997). This risk may be determined by quantifying gene flow and genetic diversity in animal species across fire mosaics. Other factors that may influence gene flow such as population density (Konvicka *et al.* 2012), topography (Cushman *et al.* 2006) and geographic distance (Wright 1943) can be incorporated into landscape genetics analyses, with fire mosaics, to understand the factors influencing genetic structure (Cushman & Landguth 2010). This approach has shown how fire influences genetic diversity and spatial genetic structure of some animal species (Brown *et al.* 2013; Schrey *et al.* 2011a; Spear & Storfer 2010). For example, in early successional species, limited genetic structure at large spatial scales suggests that high dispersal rates allow rapid colonisation of recently burnt habitats (Pereoglou *et al.* 2013; Pierson *et al.* 2013). Investigations in a wider range of taxa and landscapes are needed to help develop generalised models to explain how fire affects genetic diversity in natural populations (Banks *et al.* 2013).

If fire causes local extinction, dispersal from surrounding unburnt habitat is essential for re-establishment (Holland & Bennett 2011). Dispersal may be less important if re-establishment is initiated by survivors of the fire (Banks *et al.* 2011; Peakall & Lindenmayer 2006). The mode by which animal populations re-establish after fire is largely unknown (Clarke 2008). Genetic studies could fill this knowledge gap and provide guidance for the spatial scales of fire management that allow species persistence in a landscape (Driscoll *et al.* 2010).

Displacement following habitat disturbance, such as fire, can alter social and mating systems and thus the genetic structure of animal populations (DiBattista *et al.* 2011; Schrey *et al.* 2011b). Areas surrounding burnt habitat could experience increased immigration of displaced animals (Banks *et al.* 2012). Untangling effects of long term habitat succession from effects of an initial displacement after fire may be difficult with 'snap-shot' space-for-time studies (Driscoll & Hardy 2005; Porter 1999). Although rarely done, monitoring change in population structure over time more powerfully assesses the impact of fire on animal populations (Driscoll *et al.* 2010). Combining spatial and temporal sampling approaches may provide an efficient compromise for examining population structure under complex fire regimes.

We used spatio-temporal sampling and landscape genetics analyses to investigate initial and long-term impacts of fire regimes on the population genetic structure of two Australian lizard species (*Amphibolurus norrisi* (Agamidae) and *Ctenotus atlas* (Scincidae)). Both are generally more abundant in late successional vegetation and decline in abundance after fire (Driscoll & Henderson 2008; Driscoll *et al.* 2012; Smith *et al.* 2013). However, their post-fire recovery varies regionally, involving factors other than simply time since fire (Driscoll & Henderson 2008; Driscoll *et al.* 2012; Smith *et al.* 2013). To incorporate this regional variation, we replicated our study in four independent landscapes; a necessary but often overlooked approach in landscape genetics (Short Bull *et al.* 2011). We characterised fire regimes by fire frequency and time since fire, and also investigated effects of population density and topography on gene flow. By comparing the genetic structure of two different lizard species, we sought to provide insights into how different life histories might influence population responses to fire. Fire may have a greater effect on social structure and thus genetic diversity in agamid lizards that have more complex social and territory structure than skinks (Martins 1994; Stamps 1983). We asked four questions (Table 1):

1. Does spatial variation in fire regime, topography and population density influence gene flow and genetic diversity?
2. Is there an immediate, temporal effect of fire in the landscape on genetic structure?
3. Is post-fire re-establishment facilitated by survivors, or by immigration from unburnt habitat?
4. Can effects of fire on genetic diversity be explained by differences in demographic attributes such as age structure, sex ratio, social and mating system or sex biased dispersal?

Methods

Study region & target species

We sampled four conservation reserves on Eyre Peninsula, South Australia (Fig. 1): Hincks Wilderness Area (33°45' S, 136°03' E; 66,658 ha), Pinkawillinie Conservation Park (32°54' S, 135°53' E; 130,148 ha), Munyaroo Conservation Park (33° 21' S, 137° 12' E; 20,139 ha) and Heggaton Conservation Reserve (33°22' S, 136°31' E; 6,476 ha). The region has an average annual rainfall between 296 mm and 361 mm. The main topographic features are white sand dunes, occurring in large, parabolic fields or longitudinal ridges interspersed by hard, reddish-brown swales (Twidale & Campbell 1985). The dominant vegetation in all reserves is low (<6 m) mallee woodland, characterised by multi-stemmed *Eucalyptus spp.* (*E. costata* and *E. socialis*), commonly associated with *Melaleuca uncinata*, *Callitris verrucosa* and *Triodia irritans* (Specht 1972). Large, severe wildfires occur on a 10-100 year time scale, commonly ignited by summer lighting (Bradstock & Cohn 2002).

Amphibolurus norrisi and *C. atlas* are both common in mallee of southern Australia (Wilson & Swan 2010). *Amphibolurus norrisi*, absent from Pinkawillinie, was sampled from three reserves only (Fig.

1). With increasing time since fire (TSF), the semi-arboreal *A. norrisi* increases in abundance at Heggaton (Driscoll & Henderson 2008) but is unaffected at Hincks (Smith *et al.* 2013). The reason for this regional variation is currently unknown. *Ctenotus atlas* inhabits *Triodia* grasses (Pianka 1969) which peak in density approximately 30 years after fire (Haslem *et al.* 2011). Population recovery after fire in *C. atlas* is likely driven by variation in rainfall and grazing that interact with fire regimes to affect the distribution and abundance of *Triodia spp.* (Driscoll *et al.* 2012; Nimmo *et al.* 2012). Home range sizes in *A. norrisi* range between 0.13 and 2.03 ha (South 2010) and *C. atlas* can move on average 6 m per day (Heffernan 2008). Five other *Ctenotus* species have mean recapture distances of 7–27 m (Read 1998). Agamid lizards often defend territories and have polygynous mating systems while such complex social structure is less common in skinks (Griffiths 1999; Martins 1994; Peters & Ord 2003; Stamps 1983).

Study design & sampling strategy

We collected DNA samples from 177 *A. norrisi* and 377 *C. atlas* individuals from 38 sites within the four reserves (*A. norrisi* = 26 sites, *C. atlas* = 31 sites) (Fig. 1). We sampled over six consecutive sampling seasons (the spring/summer period when mallee lizards are most active), from Dec 2004 – Feb 2005 (season 1) to Nov 2009 – Feb 2010 (season 6) (Table S1 in Supporting information). At each site, samples were collected over one to four sampling seasons (Table S1). Sample sizes varied from one to 34 individuals per site (Fig. 1, Table S1), so many of our analyses focussed on individuals as the sampling units (e.g. Pritchard *et al.* 2000; Rousset 2000), avoiding the need for large sample sizes and for pre-defined population boundaries. Analyses focussing on the population level were restricted to subsets of the data (Table 1).

Sites were sampled from four days to 49 years after fire (Fig. 1, Table S1) and were separated by average distances (range) of 4.7 (0.3-15.2) km at Hincks, 4.7 (0.6-11.6) km at Pinkawillinie, 1.4 (0.5-

1.8) km at Munyaroo and 3.5 (0.5-6.6) km at Heggaton (Fig. 1). These distances are at a similar spatial scale to natural and prescribed fires in mallee (Bradstock & Cohn 2002) and to commonly reported extents of genetic structure in lizards (e.g. Berry *et al.* 2005; Schrey *et al.* 2011b; Smith *et al.* 2009). At Hincks, with the most complex fire history, our sample sites also spanned a range of fire frequencies (0-5 fires since 1953, Fig. S1). At five of six sample sites burned during our study, we sampled both before and after the fires (Fig. 1, Table S1). Two sites at Pinkawillinie (P3 and P4, Dec 2005) and one site at Hincks (I4, Dec 2006) were burnt by unplanned summer wildfires. One site at Hincks (I3, April 2006) and two sites at Heggaton (N4 and S4, April 2006) were burnt during prescribed fires conducted for a related study (Driscoll *et al.* 2012). The unplanned and prescribed fires were all of high severity, consuming all above ground vegetation.

Lizards were captured in pitfall traps as previously described (Smith *et al.* 2013) or hand-captured at three sites (Table S1). We used toe-clips to identify individuals upon recapture (Smith *et al.* 2013) and recorded the age (adult or juvenile) and sex of lizards collected at 'grid' sites at Hincks and Pinkawillinie (Table S1). Genetic analyses included all sampled individuals except where indicated. Blood and tissue from clipped toes were stored, respectively, on FTA paper (Whatman) and in liquid nitrogen or 5 ml ethanol/physiological saline (1:1). Lizards were processed at a field base and released the following day at the capture location.

Microsatellite DNA data

We extracted DNA from FTA paper (Smith & Burgoyne 2004) or from tissue samples using a modified Gentra kit (Qiagen). We amplified DNA at the polymorphic microsatellite DNA loci described by Smith *et al.* (2011), and used a subset of those loci that showed spatially consistent patterns of Hardy-Weinberg equilibrium and inconsequential levels of linkage disequilibrium (13 loci for *A. norrisi*: AmNo04, AmNo05, AmNo11, AmNo12, AmNo18, AmNo20, AmNo25, AmNo26, AmNo29,

AmNo30, AmNo36, AmNo37, AmNo39; nine loci for *C. atlas*: CtAt02, CtAt03, CtAt08, CtAt09, CtAt12, CtAt15, CtAt18, CtAt24, CtAt30). Samples were genotyped on an ABI 3730 instrument (Applied Biosystems) with the size standard GS500 (-250) LIZ and alleles were scored with GeneMapper 4.0 (Applied Biosystems).

Question 1. Spatial drivers of gene flow and genetic diversity

The spatial effects of fire on gene flow and genetic diversity were investigated using all of the samples and analyses of genetic diversity, genetic structure and landscape resistance (Table 1).

Genetic diversity. To determine if post-fire succession affected genetic diversity, we analysed variation in two different diversity measures: site-level allelic richness standardised for sample size (N) and individual heterozygosity. Sample sizes varied across sites so we standardised allelic richness to N = 5 to encompass the full site variation in TSF. We conducted sensitivity analyses to test whether sample size influenced effects of TSF on allelic richness. To do this, we calculated allelic richness for N = 6 to 10. As N increased, the number of sites included in the analysis decreased, so we lost power to test effects of TSF but were able to examine if the general pattern was consistent.

We used standArich (Alberto 2006) in R 3.0 (R Core Team 2013) to calculate allelic richness for each N. First, we performed multiple random reduction (Leberg 2002) for all sample sites with ≥ 5 individuals. This produced a table of randomly subsampled individuals ranging from one to the number of individuals at the sample site (Alberto 2006). We conducted 100 random subsamples for each sample size at each site (Leberg 2002). Second, we calculated allelic richness standardised for each sample size of interest (N = 5 to N = 10). We used linear mixed-effects models in the lme4 library (Bates *et al.* 2013) for R to examine the effect of TSF on allelic richness for each N. Because we sampled multiple sites within a single fire boundary, we fitted fire (a factor naming individual fire

events) as a random effect and TSF and reserve as fixed effects. We examined interactions between TSF and reserve for *C. atlas*, but not *A. norrisi* which had a smaller range of TSF values within reserves. To estimate the effect of TSF on individual genetic diversity we first calculated the proportion of typed loci that were heterozygous in each individual. We modelled heterozygosity with the same formulation as for allelic richness (including interactive effects of TSF and reserve for both species), but also included site as an additional random term to account for potential dependence among individuals at the same site.

For both the allelic richness and heterozygosity analyses, we calculated *P*-values using Wald tests (Welsh 1996). We removed interactive terms and subsequently the reserve term if they were not significant ($P > 0.05$). Parameter estimates and standard errors were obtained using the AICcmodavg package (Mazerolle 2012).

Genetic structure. Spatial patterns of genetic structure corresponding to fire mosaics could indicate that gene flow was influenced by fire history. We examined population genetic structure in each species within each reserve separately and over the entire study region to infer broader patterns of gene flow. For each data set we used two different Bayesian clustering models. One was a non-spatial model implemented in STRUCTURE 2.3.2, which uses a Markov-chain Monte Carlo (MCMC) method to first identify the number of clusters (*K*) in a sample at Hardy-Weinberg equilibrium and then assign each individual probabilistically to a cluster (Pritchard *et al.* 2000). The second was a spatial MCMC model implemented in GENELAND 3.3.0, similar to STRUCTURE but including geographic coordinates for each individual (Guillot *et al.* 2005). GENELAND is more sensitive to weak genetic structure because spatially adjacent individuals are more likely to be in the same cluster (Guillot *et al.* 2005).

We ran STRUCTURE using the admixture and correlated allele frequency models for 500,000 MCMC repetitions after a burn-in of 200,000, with five independent runs of each *K* from 1 to 8. We inferred the number of clusters in each data set by selecting the *K* with the highest mean estimated model log-likelihood across the independent runs (Pritchard *et al.* 2000). We ran GENELAND for 500,000 MCMC repetitions, allowing *K* to vary between 1 and 10. We used the Dirichlet allele frequency model because the correlated allele frequency model can overestimate *K* (Guillot *et al.* 2005) and we found it was unstable in preliminary analyses. We set spatial uncertainty of geographic coordinates to a conservatively high estimate of 1000 m to allow for large home-range movements (Read 1998; South 2010). We discarded the first 125,000 repetitions and then inferred *K* from the mode of the posterior distribution. Five independent runs were conducted to check for consistency of results.

Landscape resistance. We developed five independent landscape resistance models based on features that might influence gene flow in the two lizard species: isolation by distance, sand dune topography, population density, time since fire and fire frequency (Table 2). The landscape features we examined related to previously derived measures of habitat suitability (see Table 2) which could affect gene flow through effects on either dispersal or population density. Our overall analysis approach was to (1) calculate genetic distance between all pairs of conspecific individuals within reserves as a measure of gene flow, (2) generate values of landscape resistance between pairs for each resistance model and (3) use simple (Mantel 1967) and partial (Smouse *et al.* 1986) Mantel tests in a causal modelling framework (Cushman & Landguth 2010; Cushman *et al.* 2006; Legendre 1993) to determine the effects of each resistance model on gene flow separately.

Using SPAGEDI 1.2 (Hardy & Vekemans 2002) we calculated genetic distance between each pair of conspecific individuals as a_r, an individual analogue to F_{ST} / (1- F_{ST}) (Rousset 2000). We generated values of landscape resistance between each pair using a method based on circuit theory which takes into account all possible pathways between pairs (rather than the single, least-cost pathway

used in many studies) (McRae & Beier 2007). We compiled each resistance model on a separate raster grid with a 20 m resolution in ArcMap 10 (ESRI) and then calculated resistance between each pair for each model using CIRCUITSCAPE 3.5.4 (McRae & Beier 2007). We defined the extent of our study landscapes with a 500 m buffer around the samples to encompass movement distances for both species (South 2010). We repeated the analysis using a 5 km buffer to encompass potential longer dispersals (Hoehn *et al.* 2007; Templeton *et al.* 2011) but found no meaningful effects of changing the buffer distance so only report results from the 500 m buffer analysis. The fire frequency resistance model was analysed only for Hincks with its more complex fire history (Fig. S1). At Heggaton, we conducted separate resistance analyses for samples collected before and after the 2006 prescribed fires (see Question 2). For the other three reserves, we included only samples collected after the most recent fire.

Analyses were conducted using the mantel function in the ecodist library (Goslee & Urban 2007) for R 3.0 (R Core Team 2013). *P*-values were obtained with 5000 joint randomisations of rows and columns of one matrix (Goslee & Urban 2007). For isolation by distance models, we used simple Mantel tests and one-tailed *P* values to determine significant ($\alpha = 0.05$) relationships between genetic and geographic distance within reserves (Goslee & Urban 2007). For other resistance models we used partial Mantel tests and two-tailed *P* values to determine significant relationships between genetic distance and landscape resistance, given the spatial distance between samples (Goslee & Urban 2007). When there was a significant correlation in the first partial Mantel test, we calculated the effect of the isolation by distance model on genetic distance while controlling for the landscape resistance model. Where the first partial Mantel test was significant and the second test was non-significant we inferred significant effects of that landscape resistance model on genetic distance (Cushman *et al.* 2006; Legendre 1993).

The sand dune topography model was based on elevation data sourced from the Shuttle Radar Topographic Mission one-second bare earth version of Australia (CSIRO 2011). Elevations were projected as points and interpolated with ANUDEM (Hutchinson 2011) to create digital elevation models that distinguished dunes from swales (Fig. S2). The three fire-related resistance models (TSF, fire frequency and population density) were derived from two different spatial data sets, one containing the year of the most recent fire, the other containing the number of fires since 1953 (South Australian Department for Environment, Water and Natural Resources). For the population density model we used the mean number of captures predicted from TSF (Smith *et al.* 2013) enabling us to parameterise areas we had not sampled. Estimates were available for Hincks and Pinkawillinie only, so we generated predictions for Munyaroo and Heggaton using published data (Table S2, Fig. S3). We examined the population density model of gene flow only for locations where there was a significant response to TSF (*A. norrisi* at Heggaton, *C. atlas* at Hincks and Pinkawillinie). The TSF and population density landscape models were both based on the same spatial data set derived from the most recent fire in each reserve. The difference between the models was that the TSF model examined linear effects of the number of years since fire, while the population density model allowed non-linear responses, reflecting population responses in each species (Smith *et al.* 2013).

Question 2. Immediate, temporal drivers of post-fire genetic structure

The immediate impacts of fire were investigated by comparing genetic structure before and after fire across the whole landscape at Heggaton, where we had similar numbers of pre- and post-fire samples (Fig. 1). For each species, we applied the landscape resistance analysis method described for Question 1 to the pre- and post-fire samples separately.

Question 3. Modes of post-fire re-establishment

Sources of re-establishment were investigated using samples from five of the six sites that burned during the study (Fig. 1, Table S1). We examined results from the STRUCTURE and GENELAND analyses of the whole sample within reserves, described for Question 1. If genetic structure was detectable, genetic differentiation between pre- and post-fire samples may indicate a stronger role of immigration than re-establishment from local survivors of the fire. We also applied STRUCTURE analyses separately to *C. atlas* samples from each site that burned during the study (sample sizes for *A. norrisi* were too small (≤ 7, Table S1)) to compare the sensitivity to detect genetic structure between pre- and post-fire samples.

Question 4. Demographic drivers of genetic diversity

At 'grid' sites at Hincks and Pinkawillinie (Table S1) where age and sex were recorded, we summarised proportions of adults and juveniles and proportions of adult males and adult females for each species. We used binomial generalised linear mixed models in lme4 to analyse whether the age and sex ratios were affected by TSF, reserve (for *C. atlas* only) and sampling season for each species separately. Site was fitted as a random effect. To investigate sex-biased dispersal in each species, we used simple Mantel tests of isolation by distance on data from adult males and adult females separately.

To determine if fire-related genetic patterns could be explained by demographic changes in *A. norrisi*, we simulated genetic data for two demographic scenarios using EASYPOP 2.0.1 (Balloux 2001). *Ctenotus atlas* did not have any detectable genetic structure within reserves so we did not simulate its population structure. For each scenario, we used a two-dimensional spatial model of 10 x 10 cells and generated data for 10 populations, each with 30 males and 30 females. We simulated

data for 13 independent loci, each with 18 possible allelic states (Smith *et al.* 2011). We used a two-phase mutation model, weighted with 5% infinite alleles model and 95% step-wise mutation model (Di Rienzo *et al.* 1994) and a mutation rate of 0.0001. Alleles were randomly assigned in the initial population.

First, we simulated populations with isolation by distance in males but not females to mimic the observed patterns in our empirical data. These were used to represent populations in unburnt habitat with stable social structures and mating systems. We specified a polygynous mating system (typical for agamids (Stamps 1983)) with 50% matings by subordinate males. We set the proportion of migration to 0.5 for males and 1 for females, and the mean dispersal distance to 4 for males and 12 for females. We ran the stable scenario for 20 generations, based on a generation time of 2 yr (South 2010) and 40 years since fire – relatively long unburnt habitat in our study system.

Second, we simulated populations with disrupted mating systems and increased male dispersal – a scenario which may occur immediately after fire (Banks *et al.* 2012). We specified a random mating system and set the proportion of migration to 1 and the mean dispersal distance to 12 for both sexes. We ran the disturbed scenario for two generations to represent populations in the first four years after fire.

We simulated 20 replicates of each scenario to determine consistency in results, calculated mean allelic richness, and used simple Mantel tests to test for isolation by distance among simulated populations.

Results

Question 1. Spatial drivers of gene flow and genetic diversity

Genetic diversity. Each species showed significant main effects of TSF on allelic richness, standardised to a sample size of five individuals. Allelic richness increased with TSF in *C. atlas* (P = 0.037, Fig. 2a) and decreased with TSF in *A. norrisi* (P = 0.003, Fig. 2b). In *A. norrisi*, but not *C. atlas*, there were also main effects of reserve, with Munyaroo having significantly lower allelic richness than Hincks and Pinkawillinie (P < 0.001, Fig. 2c). Sensitivity analyses showed consistent significant effects of TSF on allelic richness across all sample size standardisations except N = 7 (P = 0.09) and 10 (P = 0.07) for *C. atlas* (Table S3, Fig. S4, Fig. S5). The reserve effect on allelic richness in *A. norrisi* disappeared when N > 6 because it was driven by the site at Munyaroo which had only six individuals. There were no effects of TSF or reserve on individual heterozygosity in either species.

Genetic structure. Both within each reserve and across the whole study region, STRUCTURE indicated that all conspecific individuals belonged to a single genetic cluster (Fig. S6). However, GENELAND suggested that *C. atlas* individuals at Hincks were genetically different from those at the other reserves (Fig. 3a, Fig. S7), although assignment probabilities were always < 71 % suggesting only weak differentiation (Fig. 3a). One 'ghost' cluster (Guillot *et al.* 2005) to which no individuals were assigned was also identified (the dark band at the bottom of Fig. 3a). For *A. norrisi*, GENELAND results indicated that individuals at N3 and N4 (last burnt in 1960) were genetically differentiated from the other six sites at Heggaton (Fig. 3b, Fig. S7) but there was no differentiation across the fire mosaic at the southern Heggaton sites (Fig. 3b). There was no convincing evidence of genetic structure in any other data set from individual reserves or across the study region (Fig. S6, Fig. S7, Fig. S8). Thus, there was no evidence that patterns of genetic structure were related to fire regimes.

Landscape resistance. There were no significant effects of landscape resistance on genetic distance in *C. atlas* (Table S4). For *A. norrisi*, we found significant isolation by distance at Hincks (r_M = 0.128, P < 0.001) and at Heggaton, both before (r_M = 0.153, P = 0.034) and after (r_M = 0.162, P = 0.045) the 2006 fires, while at Munyaroo, there was a significant effect of the TSF model on genetic distance (r_M = 0.555, P = 0.045). There, individuals in long-unburnt habitats were more genetically different from each other than individuals in recently burnt habitat.

Question 2. Immediate, temporal drivers of post-fire genetic structure

There were no changes between the pre- and post-fire samples from Heggaton that would indicate an immediate, temporal effect of fire on landscape genetic structure (Table S4).

Question 3. Modes of post-fire re-establishment

At the sites that burned during the study, samples collected before or after fire were genetically indistinguishable, whether analysed alone or with other samples from the same reserve. Although we observed genetic differentiation at Heggaton using GENELAND (Fig. 3b), this was related to the spatial location of samples, rather than whether they were collected before or after fires.

Question 4. Demographic drivers of genetic diversity

We observed a female biased sex ratio in both species at Hincks (Table S5) but could not differentiate between a demographic effect or an effect of sex differences in capture rates. There were no significant effects of TSF, location or sampling season on age structure or sex ratio in either species.

For *A. norrisi* at Hincks we found significant isolation by distance in adult males (r_M = 0.180, P = 0.022) but not adult females (Table S4), indicating female-biased dispersal. The significant isolation by distance in the overall sample for *A. norrisi* (adults and juveniles) was unlikely to have been driven solely by relatedness among pre-dispersed juveniles because the same effect was observed in adult males. There was no evidence for sex-biased dispersal in *C. atlas* (Table S4).

Our first simulation consistently produced significant isolation by distance in males but not females (Table S6), reflecting the pattern in our empirical data. The second simulation, with a disruption of the polygynous mating system and increased male dispersal, resulted in no isolation by distance for either sex (Table S6) and an increase in mean allelic richness (first simulation = 11.8, second simulation = 17.3; t = –80.13, P < 0.001).

Discussion

We discovered contrasting effects of fire on genetic diversity in two lizard species. Allelic richness decreased with TSF in *A. norrisi* and increased in *C. atlas* (Question 1). There were no consistent effects of fire-related habitat features or topography on gene flow in either species (Question 1) but we found isolation by distance in *A. norrisi*. We found no evidence of an immediate, temporal effect of fire on gene flow in either species (Question 2) and we were unable to distinguish between survival and immigration as modes of post-fire re-establishment (Question 3). Post-fire habitat succession did not appear to affect movement or dispersal in our study species as it has in other animal species (Murphy *et al.* 2010; Templeton *et al.* 2011). In the absence of habitat resistance to gene flow, the observed effects of TSF on genetic diversity might be related to post-fire changes in social structure and mating systems (Pilot *et al.* 2010; Ross 2001) or population size (Frankham 1996) (Question 4). Alternatively, we might have had insufficient resolution in our genetic markers to

detect effects of fire on gene flow. We discuss these biological hypotheses and statistical caveats below.

Female-biased dispersal in *A. norrisi* likely reflects the territorial social structure and polygynous mating system common in agamids (Griffiths 1999; Martins 1994; Stamps 1983) and documented in the closely related *A. muricatus* (Peters & Ord 2003). Our simulations showed that short-term disruptions of this social structure can increase genetic diversity, explaining the higher allelic richness in *A. norrisi* from recently burned habitat. Disrupted social structure has caused elevated genetic diversity through increased outbreeding in lemon sharks (*Negaprion brevirostris*) following habitat loss (DiBattista *et al.* 2011) and in mountain brushtail possums (*Trichosurus cunninghami*) following fire (Banks *et al.* 2012). In *A. norrisi*, the decline in allelic richness with TSF might reflect a stabilisation of the social structure, through establishment of territories and increased relatedness among proximate individuals (e.g. Gardner *et al.* 2001). At Munyaroo, genetic distance between individuals was lower in more recently burnt habitat, supporting a hypothesis of strong social structure in long-unburnt habitat. However, we did not observe this at the other reserves so continued research of lizard movement and behaviour across fire mosaics is needed to provide further support to our hypothesis.

For *C. atlas*, increased genetic diversity with TSF might result from changing population density. Genetic diversity is positively related to population size (Frankham 1996) and fire decreases population density in *C. atlas* (Smith *et al.* 2013). However, we did not find variation in gene flow that has accompanied habitat-related changes in genetic diversity in other lizards (Berry *et al.* 2005; Hoehn *et al.* 2007; Levy *et al.* 2010). In another late-successional skink species, *Plestiodon reynoldsi*, Schrey *et al.* (2011b) reported that genetic diversity increased with TSF, reflecting changes in population density and gene flow. Increases in population size without immigration would lead to decreases in genetic diversity through genetic drift over successive generations (Lacy 1987).

Ctenotus atlas must therefore maintain gene flow as population size increases but we could not detect increased gene flow that would reduce loss of genetic diversity through genetic drift.

Maintenance of gene flow through dispersal in fire-prone ecosystems may be an adaptation to temporally dynamic habitats (Brown *et al.* 2013; Pereoglou *et al.* 2013; Pierson *et al.* 2010). Fire mosaics did not appear to form dispersal barriers in either of our study species, supporting this suggestion. This assumes we collected enough samples from across the landscape to detect barriers (Berry *et al.* 2004) and that the time between disturbance and sample collection was long enough for barriers to form (Landguth *et al.* 2010). Our study landscapes were characterised by complex fire mosaics. A more pronounced effect of fire on genetic structure might occur in more heterogeneous habitats, where entire habitat patches are burned and population bottlenecks occur (Banks *et al.* 2013).

Despite disagreement over the reliability of the causal modelling approach that we followed (Cushman *et al.* 2013; Graves *et al.* 2013; Guillot & Rousset 2013; Legendre & Fortin 2010), there are few available alternatives that circumvent the problems identified. Cushman & Landguth (2010) suggested that causal modelling can reliably identify a correct model of landscape resistance among competing hypotheses. Others have claimed poor performance of this approach because it assumes linearity between distance matrices (Legendre & Fortin 2010) and disregards information about a range of factors (mating, dispersal, inheritance) influencing gene flow (Graves *et al.* 2013). These issues may have limited our ability to detect effects of landscape resistance on gene flow. However, the weak genetic structure revealed by non-distance-based analyses (STRUCTURE) suggest that landscape resistance patterns would be difficult to detect in our study system. Cushman *et al.* (2013) found partial Mantel tests had inflated Type I error rates but low Type II error rates. This bias would have limited impact on our conclusions because most of our partial Mantel tests were insignificant.

Guillot & Rousset (2013) showed that simple Mantel tests are appropriate for analysing isolation by distance so our conclusions regarding isolation by distance in *A. norrisi* are unlikely to be biased.

Detecting temporal genetic changes to infer that fire disrupted gene flow or that re-establishment occurred through immigration might require stronger genetic structure than we found in our target species (Berry *et al.* 2004). We recommend long-term DNA sample collection in fire-prone ecosystems to develop better understanding of the effect of fire on genetic structure of natural populations. Further studies should focus on those species with limited dispersal relative to the spatial scale of fire mosaics which are likely to most be affected by fire management decisions.

By comparing two ecologically different lizard species we discovered species-specific genetic responses to post-fire habitat succession. We propose that differences in the relationship between genetic diversity and TSF resulted from differences in the influence of population density and social structure. We predict stronger effects of disturbance on genetic diversity for species with stable social organisation. Our study has shown how genetic investigations can uncover part of the mechanism that causes species to vary in their distribution and abundance under different fire regimes (Banks *et al.* 2013; Keith 2012). Combining this approach with direct ecological studies of movement and behaviour will help ensure that fire management is conducted at spatial and temporal scales appropriate for biodiversity conservation.

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Data accessibility

Appendix S1 is a spreadsheet containing the sample information, location and genotype for each individual. Input files for analyses, pairwise landscape resistance values and simulation parameters are also included.

Author contributions

ALS, CMB, MGG and DAD designed the research and collected the data; ALS analysed the data and wrote the manuscript with extensive input from CMB, MGG and DAD.

Supporting information

Additional supporting information may be found in the online version of this article:

Table S1 Sites where DNA samples from *Amphibolurus norrisi* and *Ctenotus atlas* were collected on the Eyre Peninsula, South Australia.

Fig. S1 A spatial mosaic of different fire frequencies at Hincks.

Fig. S2 A digital elevation model used to test the effect of sand dunes on gene flow in *Amphibolurus norrisi* and *Ctenotus atlas*.

Table S2 Results from generalised linear mixed models investigating the effect of time since fire on capture rates in *Amphibolurus norrisi* and *Ctenotus atlas* at Munyaroo and Heggaton.

Fig. S3 The effect of time since fire on capture rates in *Amphibolurus norrisi* and *Ctenotus atlas* at Munyaroo and Heggaton.

Table S3 Results from linear mixed models to examine the effect of time since fire and reserve on allelic richness in *Amphibolurus norrisi* and *Ctenotus atlas*.

Fig. S4 Results from a sensitivity analysis to test how changing the sample size standardisation influenced the effect of time since fire on allelic richness in *Ctenotus atlas*.

Fig. S5 Results from a sensitivity analysis to test how changing the sample size standardisation influenced the effect of time since fire on allelic richness in *Amphibolurus norrisi*.

Fig. S6 Results from STRUCTURE indicating the most likely number of clusters in the samples from *Amphibolurus norrisi* and *Ctenotus atlas*.

Fig. S7 Results from GENELAND indicating the most likely number of clusters in the samples from *Amphibolurus norrisi* and *Ctenotus atlas*.

Fig. S8 Probabilities of assignment to genetic clusters identified by GENELAND.

Table S4 Results from causal modelling of the effect of landscape resistance on genetic distance in *Amphibolurus norrisi* and *Ctenotus atlas*.

Table S5 Age and sex structure of *Amphibolurus norrisi* and *Ctenotus atlas* at Hincks and Pinkawillinie.

Table S6 Mantel tests for isolation by distance and allelic richness from data simulated under a stable demographic scenario and a disturbed scenario.

Appendix S1 A spreadsheet containing the sample information, genotype data and input files for analyses.

Figure legends

Fig. 1 Samples from *Amphibolurus norrisi* and *Ctenotus atlas* were collected from 38 sites across fire mosaics in four conservation reserves on the Eyre Peninsula, South Australia. At Heggaton, we used both spatial and temporal sampling strategies as similar sample sizes were collected across the landscape before (*A. norrisi* = 20; *C. atlas* = 21) and after (*A. norrisi* = 21; *C. atlas* = 22) prescribed fires in April 2006. At the other three reserves, samples were collected after the most recent fire (Hincks: Dec 2006; Pinkawillinie: Dec 2005; Munyaroo: Oct 1990), except at two sites each at Hincks and Pinkawillinie where samples were collected before and after fires (before/after sample sizes indicated as N/N).

Fig. 2 The effect of time since fire on allelic richness in (A) *Ctenotus atlas* ($P = 0.037$) and (B) *Amphibolurus norrisi* ($P = 0.003$) and (C) the effect of reserve on allelic richness in *A. norrisi* ($P < 0.001$). All results are from a standardised sample size of five individuals. Model estimates are shown over the data in A and B (open circles = Heggaton; closed circles = Hincks; closed triangles = Munyaroo; open triangles = Pinkawillinie). Error bars are 95 % confidence intervals.

Fig. 3 Probabilities of assignment to genetic clusters identified by GENELAND (each bar represents an individual lizard). Plots are shown only for data sets in which genetic differentiation was detected. (A) Differentiation between Hincks at the other reserves was evident for *C. atlas* and (B) a distinct cluster was formed by N3 and N4 within Heggaton for *A. norrisi*. For Heggaton, the site name and year of last fire is shown below the bars and whether samples were collected (b) before or (a) after the prescribed fires is shown above the bars.

Table 1 Analytical techniques used to answer our four research questions

Method	**Data set**	**Level**
Question 1. Does spatial variation in fire, topography and population density influence gene flow and genetic diversity?		
Linear-mixed models of time since fire effects on allelic richness	Sample sites with ≥ 5 individuals	Population
Linear-mixed models of time since fire effects on individual heterozygosity	All samples	Individual
STRUCTURE	All samples	Individual
GENELAND	All samples	Individual
Simple and partial Mantel tests of the effects of landscape resistance on genetic distance	All samples except pre-2005/2006 fire samples at Hincks and Pinkawillinie	Individual
Question 2. Is there an immediate, temporal effect of fire in the landscape on genetic structure?		
Simple and partial Mantel tests of the effects of landscape resistance on genetic distance	Heggaton samples pre- and post-fire	Individual

Question 3. Is post-fire re-establishment facilitated by survivors, or by immigration?		
STRUCTURE analysis on samples within the overall sample and on each site separately	Five sites (two at Hincks, two at Pinkawillinie and one at Heggaton) where samples were collected before and after fires that occurred during the study	Individual
Question 4. Can affects of fire on genetic diversity be explained by differences in demographic attributes?		
Generalised linear mixed models of time since fire effects on population age structure and sex ratios	'Grid' sites at Hincks and Pinkawillinie (Table S1) where age and sex were recorded	Population
Simple Mantel tests of isolation by distance in adult males and adult females separately (sex-biased dispersal)	'Grid' sites at Hincks and Pinkawillinie (Table S1) where age and sex were recorded	Individual
EASYPOP simulations of genetic data for stable and disturbed *A. norrisi* populations	Simulated microsatellite data	Population

Table 2 Five spatial models of landscape resistance based on features that could affect gene flow in *Amphibolurus norrisi* and *Ctenotus atlas*

Spatial model	**Grid cell values**	**Potential ecological importance**
Isolation by distance	1	Genetic distance can increase with geographic distance (Wright 1943).
Sand dune topography	Metres above sea level	*Amphibolurus norrisi* has been recorded more commonly on dunes than swales (South 2010) and *C. atlas* depends on *Triodia spp*. which occur on deep sands (Pianka 1972). Gene flow may be inhibited or promoted by sand dunes if the dunes affect their dispersal ability or population density.
Time since fire (TSF)	Number of years since most recent fire (1-54)	Marked changes in vegetation structure occur with TSF at our study sites (Smith *et al.* 2012) and habitat structure can affect dispersal and population density in lizards (Berry *et al.* 2005; Templeton *et al.* 2011).

		This model test whether gene flow is affected by TSF in a linear way.
Population density	Mean no. captures predicted from TSF (Smith *et al.* 2013)	Habitat suitability for lizards does not always change linearly with TSF (Nimmo *et al.* 2012; Smith *et al.* 2013). Dispersal through unsuitable habitat may be inhibited (Prevedello *et al.* 2010; Shanahan *et al.* 2011) or promoted (Driscoll & Hardy 2005; Schtickzelle *et al.* 2007) and increased population density can positively or negatively affect gene flow (Robinet *et al.* 2008; Stephens *et al.* 1999).
Fire frequency	Number of fires since 1953 (0-5)	Fire can have cumulative effects on animal populations (Lindenmayer *et al.* 2008) either through demographic impacts of repeated burning (Westgate *et al.* 2012) or changes in habitat structure (Pausas & Lloret 2007).